

SENSITIVITY OF FITNESS TO VARIATION IN ITS COMPONENTS IN *DROSOPHILA STURTEVANTI* (DIPTERA, DROSOPHILIDAE)

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ABSTRACT

An evaluation was made of total fitness and the contribution of variation in fitness components on total fitness of four strains and their 12 reciprocal crosses of *Drosophila sturtevanti* Duda, 1927. The strain from Brazil presents standard arrangement in all chromosomes and the other three (from Colombia, Costa Rica and Mexico) present the same four homozygous inversions in chromosomes II and III. For each strain and its crosses 12 metric traits of the larval and the adult stages were studied. Data were used to compose fitness indices, proposed as representative of total fitness, and to estimate the effect of variation in each component on total fitness. The diversity of the fitness index values showed that the inversions and the standard arrangement had different expressions in the composition of total fitness; it also showed that equally high total fitness values could be due to high value components for larval or adult stages. The results also demonstrated the occurrence of trade-offs in the expression of fitness components which are considered as adaptive strategies.

KEYWORDS. Total fitness, adaptive strategies, life history traits, trade-offs.

INTRODUCTION

Many studies report genotype specific fitness or fitness components considering only one stage of the life cycle; studies that consider only a small number of fitness components may overlook others that could be fundamental to the understanding of genotypic differences relating to total fitness. According to HEDRICK & MURRAY (1983), there is no assurance that a genotype which is favored as to one fitness component will be

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similarly favored as to the another. Studies made with populations of *D. melanogaster* Meigen, 1830, suggested variation in fitness components of the larval stage, to a variable degree, to be less important than those of the adult stage, and that mating success or fertility have major contributions (PROUT, 1971; BUNDGAARD & CHRISTIANSEN, 1972). Also ANDERSON *et al.* (1979), studying genetic load in *D. melanogaster*, BRITTNACHER (1981), studying inversions of chromosome III in *D. pseudoobscura* Frolova, 1929, and EHRMAN & PARSONS (1976), showed that male mating success largely determines lifetime reproductive success of male. In an attempt to establish the relative importance of variation in fitness components in different stages of the life cycle of *D. melanogaster*, HIRAIZUMI (1961) considered that lifetime reproductive success is most sensitive to variation in development rate and fertility, in the pre-adult and adult stages, respectively. But, as shown by BARNES & MERRELL (1985), the relative importance of larval or adult components could be subordinated to the degree of adaptation to the environment considered.

Prediction of responses to natural selection requires the identification of many characters which together comprise fitness, their phenotypic and genetic variances and covariances with fitness and with each other. This study considers such a question proposing that the construction of an index would enable to predict not only the population response to natural selection in different habitats, in which the relative weights of the components may vary, but also the evolution of the component characters as a correlated response, as proposed by MACKAY (1985). Total fitness of *D. sturtevantii* Duda, 1927, was first broken down into several metric components of pre-adult and adult stages, followed by the combination of their measures in a single value which is proposed as representative of total fitness. This procedure makes it possible to compare the four strains and all types of offspring of their crosses according to their total fitness values. It also makes possible the estimation of total fitness sensitivity to variation in its components and to propose the occurrence of trade-offs in this variation as patterns of adaptive strategies.

MATERIAL AND METHODS

The following four strains of *Drosophila sturtevantii* Duda, 1927 were used: one with the standard arrangement in all chromosomes (BRABRA) and the other three (COLCOL, COSCOS and MEXMEX) with the standard X chromosome arrangement and the same four homozygous inversions (A, B, C and F) in chromosomes II and III, comprising 22% of the genome (HOSAKI, 1986). The strain BRABRA was prepared with 18 flies collected in Mirassol (SP, Brazil), in 1971, by W.J. Tadei. The strain MEXMEX was prepared with 40 females and nine males, collected in Veracruz (VER, Mexico), in 1975, by A.J. Gallo and V.M. Salceda. The strains, here called COLCOL and COSCOS have been maintained since 1967 at the Laboratory of Populations "Prof. Dr. Celso Abbade Mourão" (Department of Biology, IBILCE- UNESP, São José do Rio Preto), and were derived from stocks brought from the Genetics Foundation (University of Texas, Austin, USA), respectively labeled as "H 193.3" (Villavicencio, Colombia) and "H158.1" (Turrialba, Costa Rica).

The four strains were intracrossed and intercrossed in all combinations to produce offspring with three different chromosomal constitutions (tab. I) as follows: (i) four structural homozygotes, with chromosomes of the same geographic origin (parental strains 1 to 4); (ii) six structural heterozygotes (offspring 5 to 10) and (iii) six structural homozygotes for inversions but heterozygotes for geographic origin of each set of chromosomes (offspring 11 to 16). Five groups of 10 couples each, from each cross, seven days old, were put into vials (2cm diameter x 10cm height) and observed for sexual activity. The best age for crosses in this species is the 7th day, before which few flies are able to mate (DOBZHANSKY, 1944). As *D. sturtevantii* normally presents single mating during the time interval considered for this study, and couples remain still in the same place, almost unmoving during the mating, we were able to observe 10 couples at a time over 90 minutes, at 25°C. For each couple, the beginning and end of the mating was recorded. After 90 minutes, the 10 couples of each of the five vials from each parental strains and their hybrids were transferred to bottles with fresh corn-wheat-arrowroot medium.

Five other similar bottles, with 10 couples also seven days old were prepared, totaling 10 replicates of mass crosses. Flies were maintained 3.5 days in these first bottles for oviposition and then transferred to new bottles twice for another two periods 3.5 days each, resulting in 30 bottles per parental strain and per each hybrid. Dead flies were replaced at each transfer with others taken from extra bottles prepared at the same time and exactly the same way as the experimental ones. Thus, the density of 10 couples at the beginning of each half week of oviposition period was maintained. Each bottle was daily observed and the day of the appearance of the first pupa and of the first imago was recorded. Flies were counted every half week after adult emergence began; the last counting was done when the emergence ceased or at the latest on 35th day after the cross date. After counting, males and females from each bottle were separately weighed. The pupae were also counted (CARARETO & MOURÃO, 1992).

Table I. Parental and genetic constitutions produced by intra and intercrosses among four parental strains of *Drosophila sturtevantii* (1 to 16 as defined in Material and Methods).

	Female			
Male	BRABRA	COLCOL	COSCOS	MEXMEX
BRABRA	(1) BRABRA	(5) BRACOL	(7) BRACOS	(9) BRAMEX
COLCOL	(6) COLBRA	(2) COLCOL	(11) COLCOS	(13) COLMEX
COSCOS	(8) COSBRA	(12) COSCOL	(3) COSCOS	(15) COSMEX
MEXMEX	(10) MEXBRA	(14) MEXCOL	(16) MEXCOS	(4) MEXMEX

The experimental procedure enabled the study of 12 metric traits, from three stages of life cycle, for each strain and their 12 crosses. The 16 groups of genotypes are here called genetic constitutions (GC1 to GC16). The so-called Sexual Activity Stage (SA) was broken down into three traits related to the sexual activity performed by 10 couples, in 5 vials: (1) mating frequency (MF); (2) duration of pre-copula (DPC), taken as the time interval between the beginning of the observation of the vial and each copula; (3) duration of copula (DC), taken as the time interval during which the male remained over the female. The Progeny Stage (P) was broken down into five traits related to the emerged individuals in each of the 30 bottles: (4) total number of imagines (NI); (5) number of imagines in the first counting (NIFC); (6) number of pupae (NP); and (7) female individual biomass (FB), and (8) male individual biomass (MB), measured in milligrams. The Time of Development Stage (TD), measured in days, was broken down into four traits: (9) egg-to-pupa time of development (EPTD); (10) egg-to-imago time of development (EITD); (11) pupa-to-imago time of development (PITD); and (12) duration of the emergence period (DEP). The means and the standard errors of these traits, were published in CARARETO & MOURÃO (1992). Here we are analyzing the means of these traits (tab. II) to generate fitness indices representative of total fitness (W). We also aim to estimate the sensitivity of total fitness to these various fitness components.

To obtain fitness indices, we calculated a geometric mean of the 16 mean values of each trait (tab. II) that were firstly transformed to a logarithm scale. Then, for the 12 traits, each mean value was calculated as a percentage of the respective geometric mean, as illustrated below.

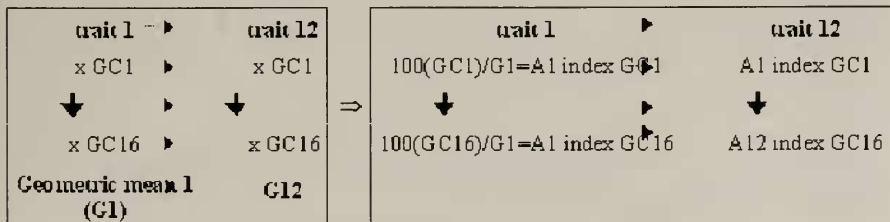


Table II. Means for 12 fitness components of four parental strains of *Drosophila sturtevantii* and offspring of their intercrosses, measured at 25°C (MF, mating frequency; DPC, duration of pre-copula; DC, duration of the copula; NI, number of imagines; NIFC, number of imagines in the first counting; NP, number of pupae; FB, female individual biomass; MB, male individual biomass; EPTD, egg-pupae time of development, EITD, egg-imagino time of development, PITD, pupa-imagino time of development; DEP, duration of emergence period; biomass measured in milligrams; time of development measured in days).

Component	BRABRA	COLCOL	COSCOS	MEXMEX	BRACOL	COLBRA	BRACOS	COBIRA	BRAMEX	MEXBRA	COLCOS	COSCOL	COLMEX	MEXCOL	COSMEX	MEXCOS
MF	25.0	34.0	37.0	55.0	31.0	38.0	40.0	38.0	39.0	37.0	40.0	39.0	47.0	39.0	45.0	49.0
DPC	19.0	37.8	15.6	24.6	35.1	11.0	27.1	15.1	22.4	19.2	12.2	31.7	26.0	30.4	13.2	11.0
DC	12.5	8.8	10.5	11.5	11.4	13.8	11.3	12.5	16.7	11.4	13.0	11.7	12.7	11.2	12.1	12.7
NI	252.0	254.0	318.0	242.0	357.0	339.0	307.0	346.0	274.0	257.0	312.0	304.0	272.0	303.0	237.0	253.0
NIFC	12.0	63.9	33.3	24.7	27.0	32.0	30.6	10.9	12.0	12.4	30.7	24.0	41.6	30.6	6.8	10.4
NP	272.0	316.0	437.0	395.0	430.0	452.0	477.0	580.0	468.0	479.0	533.0	537.0	458.0	501.0	563.0	540.0
FB	1.31	1.34	1.26	1.34	1.24	1.25	1.24	1.26	1.30	1.32	1.25	1.26	1.35	1.29	1.33	1.4
MB	0.93	1.03	1.01	1.08	0.88	0.89	0.99	0.96	0.98	0.97	0.97	0.99	1.04	1.00	1.06	1.11
EPTD	11.2	8.4	9.4	9.4	9.3	9.5	8.8	9.7	9.2	9.6	8.9	9.0	9.0	9.0	9.5	9.1
EITD	19.6	17.7	20.0	23.1	20.2	20.7	21.5	23.3	23.7	23.4	21.4	21.1	21.3	22.4	24.9	24.6
PITD	8.5	9.3	10.6	13.8	10.9	11.2	12.7	13.6	14.4	13.8	12.5	12.1	12.3	13.4	15.4	15.4
DEP	7.9	8.9	12.0	14.5	11.4	12.9	13.2	15.0	15.6	14.5	13.0	12.7	13.7	14.6	15.6	15.9

These values, denominated **A** indices (tab. III), compare each mean value of each trait to the geometric mean of the 16 genetic constitutions. Thus, mean value similar to the geometric mean originates **A** index around 100 and mean values above or below the geometric mean originate indices bigger or smaller than 100, respectively. These indices were used to compose fitness indices, assuming a multiplicative effect for traits (SVED *et al.*, 1967), to each stage (SA', P', TD' indices) and to the proposed total fitness index (W').

To obtain W' index, the indices of each stage were transformed into decimals and then multiplied as direct or inverted ratios, based on the following assumptions: (1) for SA' fitness index: high mating frequency and high duration of copula are better than low values for these components, since a larger number of females can yield progeny and more time is available for male gamete transfer; for the duration of pre-copula, lower values mean greater efficiency, i.e., faster mating; (2) for P' fitness index: higher values mean greater efficiency because they correspond to more offspring and more efficiency in converting food into vital substance; (3) for TD' fitness index: lower values mean greater efficiency, that is, faster life-cycle, since a lineage could be produced more quickly. Thus, the fitness components numbered as 1 and 4 to 8 were computed as direct ratios and all the others as inverted ratios, so that: SA'=(MF)(1/DPC)(1/DC) (1); P'=(NI)(NIFC)(NP)(MB)(BF) (2); TD'=(1/EPTD)(1/EITD)(1/PITD)(1/DIEP) (3); W'=(SA')(P')(TD') (4).

To evaluate the importance of variation in fitness components to total fitness (W'), we estimated the contribution degree of each component transforming into decimals the 12 **A** indices of each genetic constitution, summing them in their direct or inverted ratios, due to the assumptions mentioned above, and then, computing each one as a percentage of the respective sum (tab. IV). These 192 values, denominated as **B** indices, estimate the relative degree as each trait contribute to compose the total fitness (W'), as illustrated below.

Correlation analysis between each pair of the 16 genetic constitutions was made, using the 12 **B** indices of each one, as a procedure to compare each with one another as to the relative importance of each trait's contribution to total fitness (W') composition. As we performed multiple linear correlation tests, the critical α value used was 0.0005, according to the Sequential Bonferroni Correction Technique (RICE, 1989).

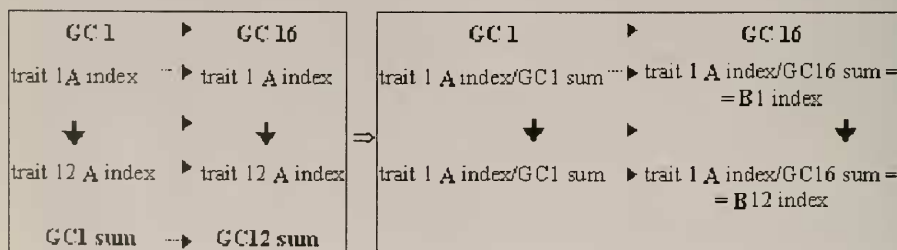


Table III. A indices for 12 fitness components of four parental strains of *Drosophila sturtevanti* and offspring of their intercrosses (MF, mating frequency; DPC, duration of pre-copula; DC, duration of copula; NI, number of imagines; NIFC, number of imagines in the first counting; NP, number of pupae; FB, female individual biomass; MB, male individual biomass; EPTD, egg-pupae time of development, EITD, egg-imago time of development, PITD, pupa-imago time of development; DEP, duration of emergence period; biomass measured in milligrams; time of development measured in days).

Component	BRABRA	COLCOL	COSCOS	MEXMEX	BRACOL	COLBRA	BRACOS	COSBRA	BRAMEX	MEXBRA	COLCOS	COSCOL	COLMEX	MEXCOL	COSMEX	MEXCOS
MF	64.2	87.3	95.0	141.2	79.6	97.5	102.7	97.5	100.1	95.0	102.7	100.1	120.6	100.1	115.5	125.8
DPC	93.6	186.2	76.9	121.2	172.9	54.2	133.5	74.4	110.4	94.6	60.1	156.2	128.1	149.8	65.0	54.2
DC	104.1	73.3	87.4	95.8	94.9	114.9	94.1	104.1	139.1	94.9	108.3	97.4	105.8	93.3	100.8	105.8
NI	87.9	88.6	110.9	84.4	124.5	118.2	107.1	120.7	95.6	89.6	108.8	106.0	94.9	105.7	82.6	88.2
NIFC	56.3	300.0	156.3	116.0	126.8	150.2	143.7	51.2	56.3	58.2	144.1	112.7	195.3	143.7	31.9	48.8
NP	59.6	69.2	95.7	86.5	94.2	96.0	104.5	127.0	102.5	104.9	116.7	117.6	100.3	109.7	123.3	118.3
FB	101.2	103.5	97.3	103.5	95.8	96.5	95.8	97.3	100.4	101.9	96.5	97.3	104.2	96.6	102.7	108.1
MB	93.8	103.9	101.9	109.0	88.8	89.8	99.9	96.9	98.9	97.9	97.9	99.9	104.9	100.9	107.0	112.0
EPTD	120.5	90.4	101.1	101.1	100.1	102.2	94.7	104.4	99.0	103.3	95.8	96.8	96.8	96.8	102.2	97.9
EITD	90.2	81.5	92.1	106.3	93.0	95.3	99.0	107.7	109.1	107.7	98.5	97.1	98.1	103.1	114.6	113.2
PITD	68.9	75.4	85.9	111.9	88.4	90.8	103.0	110.3	116.8	111.9	101.4	98.1	99.7	108.7	124.9	124.9
DEP	60.8	68.5	92.4	111.6	87.7	99.3	101.6	115.4	120.1	111.6	100.0	97.7	105.4	112.4	120.1	122.4

Table IV. B indices for 12 fitness components of four parental strains of *Drosophila sturtevanti* and offspring of their intercrosses (MF, mating frequency; DPC, duration of pre-copula; DC, duration of copula; NI, number of imagines; NIFC, number of imagines in the first counting; NP, number of pupae; FB, female individual biomass; MB, male individual biomass; EPTD, egg-pupae time of development, EITD, egg-imago time of development, PITD, pupa-imago time of development; DEP, duration of emergence period; biomass measured in milligrams; time of development measured in days).

Component	BRABRA	COLCOL	COSCOS	MEXMEX	BRACOL	COLBRA	BRACOS	COSBRA	BRAMEX	MEXBRA	COLCOS	COSCOL	COLMEX	MEXCOL	COSMEX	MEXCOS
MF	5.49	6.00	7.12	11.77	6.59	7.30	8.30	8.21	9.29	8.43	7.71	8.27	9.33	8.24	9.92	10.20
DPC	9.14	3.69	9.76	6.88	4.79	13.81	6.06	11.32	8.41	9.38	12.51	5.29	6.04	5.50	13.21	14.97
DC	8.22	9.38	8.57	8.71	8.72	6.51	8.59	8.09	6.67	9.34	6.94	8.48	7.31	8.82	8.52	7.67
NI	7.52	6.09	8.31	7.04	10.31	8.85	8.66	10.16	8.86	7.95	8.18	8.76	7.33	8.70	7.10	7.16
NIFC	4.82	20.62	11.72	9.67	10.50	11.24	11.62	4.31	5.23	5.16	10.84	9.31	15.10	11.83	2.74	3.96
NP	5.09	4.76	7.18	7.21	7.80	7.41	8.45	10.70	9.51	9.31	8.78	9.71	7.76	9.03	10.59	9.60
FB	8.65	7.11	7.30	8.63	7.93	7.22	7.74	8.19	9.31	9.04	7.26	8.04	8.06	8.20	8.82	8.77
BM	8.03	7.14	7.64	9.09	7.36	6.72	8.08	8.16	9.17	8.68	7.36	8.25	8.11	8.31	9.19	9.09
EPTD	7.10	7.61	7.41	8.24	8.28	7.32	8.54	8.07	9.37	8.59	7.85	8.53	7.99	8.50	8.40	8.29
EITD	9.48	8.44	8.14	7.84	8.91	7.85	8.17	7.85	8.50	8.24	7.63	8.50	7.89	7.98	7.49	7.16
PITD	12.41	9.12	8.72	7.45	9.37	8.24	7.85	7.64	7.95	7.93	7.42	8.42	7.75	7.58	6.88	6.50
DEP	14.07	10.04	8.12	7.47	9.44	7.54	7.96	7.29	7.73	7.95	7.51	8.45	7.33	7.32	7.15	6.63

RESULTS

The W' scores, proposed as fitness indices, showed striking differences among the indices of life stage for the same genetic constitution, or among constitutions for the same life stage (tab. V). The strains COLCOL and COSCOS presented the highest W' values, and BRAMEX and COSMEX, the lowest ones. The highest COLCOL's W' is a consequence of elevated P' and TD' fitness indices which were up to four times larger than the indices of the others. These high values are a result of its NIFC's A index and EPTD's A index, respectively. These values, associated with a smaller SA index, shows COLCOL as a very differentiated strain. As in the case of the parental strain, the offspring of COLCOL crosses are in general associated with the highest P' and TD' indices and the slowest SA' , particularly if the COL chromosome complement comes from their mothers.

On the contrary of the situation showed by COLCOL strain and their offspring, the

strain MEXMEX and its offspring are associated with the lowest P' and TD' indices, except when the MEX and COL chromosomes are combined. The highest SA' index among the parental strains are associated with COSCOS and MEXMEX. The same can be observed in offspring of COS and MEX reciprocal crosses; however, their SA' indices are almost twice the parental strains. Nevertheless, when intercrossed with BRA and COL, the index values are very varied.

Table V. Fitness indices of Sexual Activity (SA'), Progeny (P') and Time of Development (TD') stages and Total Fitness (W') of four parental strains of *Drosophila sturtevanti* and offspring of their intercrosses.

Genetic Constitution	Stages			W'	
	SA'	P'	TD'	Absolute	Relative
BRABRA	0.659	0.280	2.195	0.405	0.122
COLCOL	0.639	1.978	2.629	3.325	1.000
COSCOS	1.413	1.645	1.353	3.146	0.946
MEXMEX	1.216	0.955	0.745	0.865	0.260
BRACOL	0.485	1.264	1.386	0.849	0.255
COLBRA	1.566	1.524	1.139	2.718	0.817
BRACOS	0.817	1.537	1.020	1.281	0.385
COSBRA	1.260	0.739	0.702	0.653	0.196
BRAMEX	0.652	0.548	0.661	0.236	0.071
MEXBRA	1.058	0.546	0.720	0.416	0.125
COLCOS	1.578	1.730	1.045	2.853	0.858
COSCOL	0.658	1.366	1.109	0.996	0.300
COLMEX	0.891	2.033	1.002	1.813	0.545
MEXCOL	0.717	1.674	0.820	0.984	0.296
COSMEX	1.763	0.357	0.569	0.359	0.108
MEXCOS	2.194	0.617	0.590	0.799	0.240

To compare the contribution degree of each component to total fitness, **B** indices were calculated (tab. IV). Two components are distinguished among those with frequent high variation according to the distribution of the **B** indices: duration of pre-copula and number of imagines in the first counting. Considering the 12 **B** indices, linear correlation analyses between all pairs of genetic constitutions were made. Absence of correlation was considered as indicating different expressions of the array of the traits to the total fitness between two pairs. Positive correlation was considered as proportionality in the degree of contribution, and negative correlation was considered as inverse proportionality in the contribution degree of the 12 metric traits between two genetic constitutions. From the 120 *r* values (tab. VI), 15 were considered as a strong association: the critical α value used was 0.0005 ($r=0.850$), according to the Sequential Bonferroni Correction Technique (RICE, 1989). Among these, seven pairs had positive strong values, and eight pairs presented negative strong values. From the seven positive correlations, five are between pairs of constitution with chromosomes proceeding from Colombia or between Colombia and Costa Rica, and two are between pairs with chromosomes proceeding only from Brazil, Costa Rica and Mexico (fig. 1). Chromosomes proceeding from Colombia are present in seven out of the eight pairs of genetic constitutions negatively correlated and only in one pair there are no COL chromosomes associated with: COSCOS vs BRAMEX (fig. 2). The scatter diagrams of these 12 **B** indices of pairs of genetic constitutions show that fitness components such as duration of pre-copula and number of imagines in the first counting are mostly responsible for the significance of the correlation.

If we are not extremely strict and adopt the commonly used 0.01 critical α value,

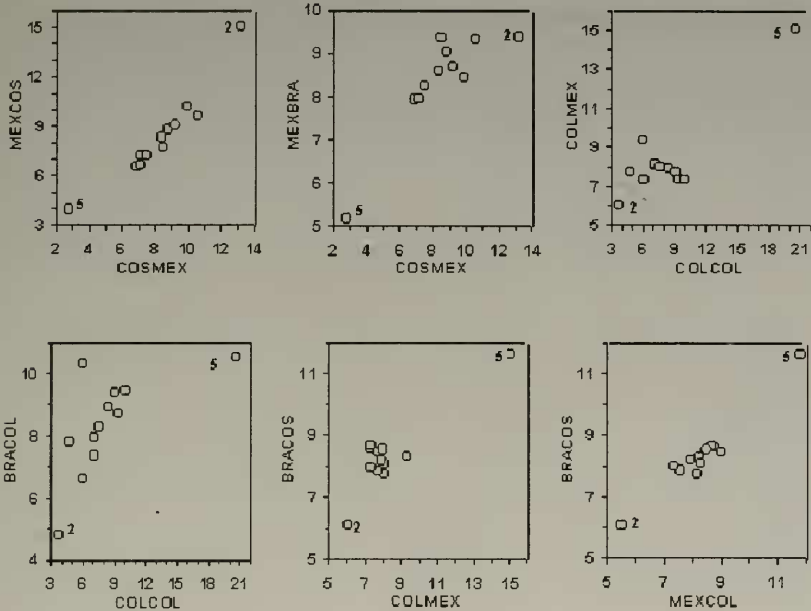


Fig 1. Scatter diagrams among **B** indices of the 12 metric traits showing positive association between genetic constitutions of four strains of *Drosophila sturtevantii* (2: DPC, 5: NIFC).

the significant value of r drops to 0.708. In such a case there are 35 significant r values: from 18 positive values, 10 are between pairs that have COL chromosomes (four of them have also COS chromosome associated), two are between pairs with COL and COS chromosomes and six of them have no COL chromosomes combined — the association is between BRA and MEX. From the 17 negatively associated pairs, 13 are between COL and non COL chromosomes (BRA and MEX in particular) and five associating non COL chromosomes (COSCOS and BRAMEX). The parental strains BRABRA and MEXMEX are never associated with their offspring.

DISCUSSION

This study has its experimental procedure devised in function of the following idea: the greater number of genotypes used in measuring the expression of the greater number of fitness components, the greater probability of revealing patterns which identify components and permit the establishment of the relative importance of its variation to total fitness.

In the present study, fitness indices, considered as representative of total fitness, were estimated by combining the fitness indices of SexualActivity, Progeny and Time of Development life stages. The total fitness indices (relative W' , tab. V) disclosed the parental strain COLCOL as the most efficient in transmitting their genes to future

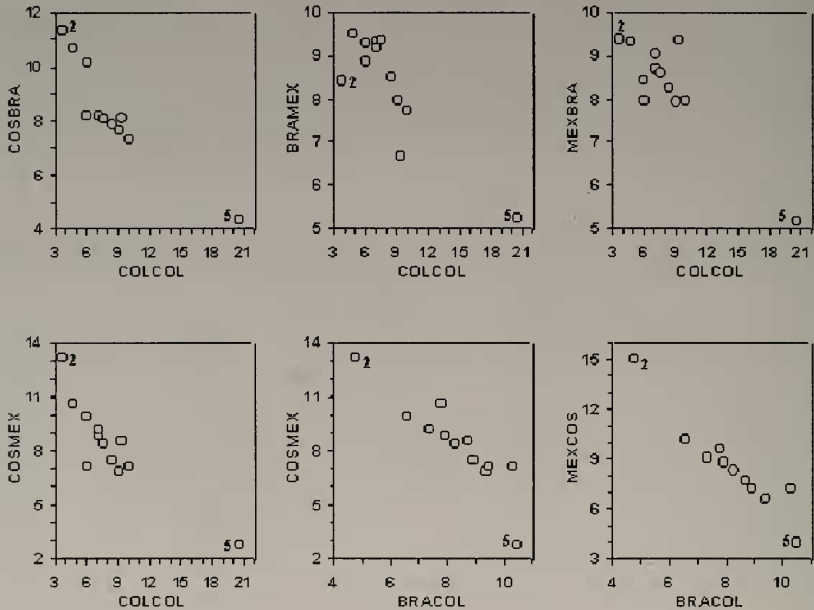


Fig 2. Scatter diagrams among **B** indices of the 12 metric traits showing negative association between genetic constitutions of four strains of *Drosophila sturtevantii* (2: DPC, 5: NIFC).

generations, followed by COSCOS, COLCOS and COLBRA. In contrast, BRAMEX, followed by COSMEX, BRABRA, MEXBRA constitutions were shown to be the worst. Although COSMEX and MEXCOS have shown greater efficacy for Sexual Activity and, COLCOL and BRABRA the greater for the Time of Development stage, the components of P' and TD' indices, with respectively very high and low values, which are considered to be favorable to gene transmission to the next generation, according to our premises, were responsible for the higher total fitness of COLCOL, exactly the less efficient strain for Sexual Activity. Different genetic constitutions presenting higher indices for different fitness stages were a recurrent situation. However, the high fitness values of COSCOS, COLCOS and COLBRA were due to a relative balance of high values for all fractions.

As the 16 genetic constitutions were produced by combining, through hybridization, four strains, three of them carrying the same chromosomal arrangement, we concluded that these arrangements and the standard one, which has no inversions (BRA), proved to be highly differentiated as to their genetic content and respective expressions in the composition of total fitness. It is noteworthy that, according to our results, these genetic contents, through interaction, are expressed differently, resulting in greatly diversified fitness values. Notwithstanding, constant effects of these genetic materials can be observed: the higher fitness indices always correspond to chromosomes COL and COS and the lowest to MEX when associated with BRA or COS chromosomes. The expression variability of the fitness components reflects the genetic variability of the gene pool studied.

Table VI Correlation coefficients (r) between the respective **B** indices of all pairs of genetic constitutions of four strains of *Drosophila sturtevantii* ($p = 0.0005$ to $r = 0.850$; $df = 10$, according to the Bonferroni sequential correction; and $p = 0.01$ to $r = 0.708$; $df = 10$)

	BRABRA	COLCOL	COSCOS	MEXMEX	BRACOL	COLBRA	BRACOS	COSBRA	BRAMEX	MEXBRA	COLCOS	COSCOL	COLMEX	MEXCOL	COSMEX
COLCOL	-0.099														
COSCOS	-0.090	0.722													
MEXMEX	-0.475	0.290	-0.055												
BRACOL	0.123	0.650	0.271	-0.113											
COLBRA	-0.065	0.154	0.747	-0.258	-0.258										
BRACOS	-0.490	0.850	0.466	0.399	0.700	-0.069									
COSBRA	-0.023	-0.906	-0.440	-0.493	-0.586	0.137	-0.741								
BRAMEX	-0.048	-0.854	-0.856	-0.101	-0.488	-0.347	-0.608	0.663							
MEXBRA	0.132	-0.890	-0.699	-0.257	-0.654	-0.291	-0.811	0.781	0.674						
COLCOS	-0.266	0.136	0.685	-0.188	-0.347	0.953	0.901	0.176	-0.294	-0.240					
COSCOL	-0.295	0.418	-0.153	0.186	0.725	-0.602	0.726	-0.436	-0.128	-0.392	-0.505				
COLMEX	-0.490	0.872	0.603	0.543	0.435	0.190	0.894	-0.785	-0.618	-0.871	0.251	0.450			
MEXCOL	-0.600	0.750	0.346	0.410	0.639	-0.165	0.972	-0.648	-0.493	-0.683	-0.061	0.772	0.847		
COSMEX	-0.015	-0.883	-0.490	-0.168	-0.903	0.089	-0.839	0.846	0.655	0.877	0.169	-0.624	-0.731	-0.747	
MEXCOS	-0.077	-0.769	-0.267	-0.118	-0.951	0.345	-0.785	0.783	0.538	0.719	0.408	-0.772	-0.584	-0.725	0.955

These expressions show positive and negative extreme effects in the composition of total fitness. Although the strains have been maintained in the laboratory under essentially identical conditions, for almost 200 (BRABRA and MEXMEX) or as much as 400 (COLCOL and COSCOS) generations, the original genetic variability has been preserved, at least in sufficient degree to permit different responses to the conditions to which the flies have been exposed. The pattern of the W' values, that shows in almost all cases that W' relative of each strain crossed with itself is higher than W' relative of crosses of the same strain with any another, argues against inbreeding depression due to long time maintenance in laboratory.

Our results contribute to understand the following question: which component is more important to determine total fitness, those of the pre-adult, or those of the adult stages (PROUT, 1971; EHRMAN & PARSONS, 1976), or both (HIRAIZUMI, 1961; POLIVANOV & ANDERSON, 1969; SVED & AYALA, 1970; SVED, 1971; TRACEY & AYALA, 1974; BARNES & MERRELL, 1985)? Considering that the SA' index is composed only by components of the adult stage; that TD' index is composed by larval components exclusively, and that the P' is composed by both larval and adult fitness components, we found that equally high total fitness values might be due to high values of traits for the larval or adult stage, depending on the genetic constitution. This assumption has been also demonstrated for only three genetic constitutions (CARARETO & MOURÃO, 1991a,b) in *Drosophila prosaltans* Duda, 1927. To MUELLER & AYALA (1981) "it is reasonable to assume that all the biological processes are important in the determination of reproductive success; however, the relative importance of each to net fitness is not clear, not even whether one or few components have a major importance". CARARETO *et al.* (1992) found significant correlation between fitness components and total fitness in *D. prosaltans*; the analysis results of the principal components showed a differential importance of components associated with number of offspring.

We calculated **B** indices aiming to evaluate the importance of each metric trait or its variation to total fitness. We also intended to compare genetic constitutions, pure or with their genetic material combined, searching for a pattern that could differentiate them according to the way their fitness components are associated to compose the total fitness.

The crossing manipulation enabled us to show that the strain from Colombia, the one with the highest W' , is very differentiated according to the pattern that its 12 traits are associated to compose its total fitness. Similar to COLCOL is the strain from Costa Rica, the second highest W' . These two strains have the larger number of positive correlation between them (tab. V). On the other hand, the strains from Brazil and from Mexico are very differentiated concerning the pattern as their 12 traits compose total fitness; compared to each other and to the other two, as indicated by the negative correlation between genetic constitutions carrying COL, BRA and MEX chromosomes. Assuming relative importance of traits as the ability to be variable, our study showed time of pre-copula and number of imagines in the first counting to be among the most relevant components to the variation of total fitness in *D. sturtevanti* strains.

The crossing manipulation provided interesting information about different fitness pattern components being combined to compose total fitness. Trade-offs are known in *D. melanogaster* between early fertility and longevity and between early and late fecundity for female (ROSE & CHARLESWORTH, 1981a,b; LUCKINBILL *et al.*, 1984; ROSE, 1984) and between early competitive mating success and longevity and late success (SERVICE, 1993). STEARNS (1992) estimated that at least 45 trade-offs have been established in life history studies and CHIPPINDALE *et al.* (1996) presented evidence for a new trade-off, manifested between larval growth rate and pre-adult viability in *D. melanogaster*. We are aware that the occurrence of trade-offs at the phenotypic level does not necessarily mean that there is an underlying antagonistic pleiotropy (REZNICK, 1985; REZNICK *et al.* 1986); otherwise, we believe that important information on trade-offs can be gathered from phenotypic manipulation, as also considered by BELL (1984 a,b), PARTRIDGE & FARQUHAR (1981) and PARTRIDGE *et al.* (1987). It seems that our hybrid crosses allowed us to characterize a new trade-off, between development rate and mating speed, which is proposed as reflecting possible patterns of adaptive strategies (figs. 1, 2).

The scatter diagrams shows only pairs of genetic constitutions strongly correlated according to their **B** indices. It is noteworthy that two pairs (fig. 1) formed by three genetic constitutions (BRAMEX, COSMEX, and MEXCOS) express a single adaptive strategy, with the perfect condition corresponding to the COSMEX-MEXCOS pair: chromosomes proceeding from Brazil and Mexico are associated with component that reflect high mating speed (short DPC) with a greater contribution to total fitness, and also with component that reflect a greater development rate (small NIFC), with a smaller contribution to total fitness. If we were not too strict in adopting the α value, following the commonly used $\alpha=0.01$, we find the same association in two more genetic constitutions (MEXBRA and COSBRA). An adaptive strategy seems to exist in relation to these chromosomes: a slower speed of development could be balanced by a greater mating speed. On the other hand, the opposite is related to COL chromosome: faster development rate associated to a slower mating speed. Several pairs of genetic constitutions (fig.1) are positively correlated according to the variation of their B indices mainly due to the greatest contribution to total fitness of NIFC and the smallest contribution of DPC (COLCOL, BRACOL, BRACOS, COLMEX, MEXCOL). This association is also illustrated (fig. 2) by genetic constitutions COLCOL, BRACOL, COLMEX, BRAMEX, MEXBRA, COSBRA, COSMEX and MEXCOS. These pairs have a common characteristic: the negative character of the association between COL and non-COL genetic constitution due to the same two extreme points (DPC with the smallest contribution and NIFC with

the greater contribution to total fitness). This second manifestation of the trade-off illustrates the adaptive strategy balancing slower mating speed by faster development rate. Again, if we were not too strict with the selected α value, eight seven pairs associating COL and non COL chromosomes corroborate this pattern (tab. VI).

Life history theory predicts that fitness should be greater for fast developing genotypes (CHARLESWORTH, 1980). Apparently the traits involved in this trade-offs are important for anticipating the following generation, since as a result of greater mating speed due to a shorter duration of pre-copula, males and females will transmit their alleles faster (FULKER, 1966; PRAKACH, 1967; SHERWIN, 1975). Precocity of emergence, expressed by a greater number of imagines in the first counting, should reflect faster development, and the early formation of the new adult generation, which is then available for mating. Associating these components maximizes the transmission efficiency of the genetic material to the following generations. The consequence may be the reduction of generation time which in the accumulation of succeeding generations results in the evolutionary advantage of a greater number of generations in a shorter time. In short, both these adaptive strategies seem to be clearly associated with the chromosome material, the former from Brazil and Mexico and the latter from Colombia. As structurally the COL, COS and MEX chromosomes are identical as they carry the same inversions, our results are evidence of genetic diversity included within the inversions and their background, greater in the COL chromosomes compared with the other two.

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